THE CALLOVIAN (MIDDLE JURASSIC) MARINE CROCODILE *METRIORHYNCHUS* FROM CENTRAL ENGLAND

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ABSTRACT. For many years the taxonomy of the Callovian marine crocodile genus *Metriorhynchus* has been in a state of confusion. Bivariate and principal coordinate analyses are used in an attempt to identify cranial characters for discriminating species. Many of the characters used previously to define eight species of *Metriorhynchus* are shown to be individually variable or continuously variable. Only two Callovian species can now be identified on the basis of their skull proportions: *M. superciliosus* incorporates specimens previously assigned to *M. superciliosum* de Blainville, 1853, *M. moreli* E. E. Deslongchamps, 1867, *M. leedsi* Andrews, 1913, and *M. laeve* Andrews, 1913; *M. brachyrhynchus* includes *M. brachyrhynchus* E. E. Deslongchamps, 1867, *Suchodus durobrivense* Lydekker, 1890, *M. cultridens* Andrews, 1913, and *M. casamiquelai* de Gasparini and Diaz, 1977.

THE current classification of the Callovian marine crocodiles of the genus *Metriorhynchus* was established largely by E. E. Deslongchamps (1863–1869) and Andrews (1913). Deslongchamps gave the first detailed descriptions and figures of *Metriorhynchus*, emending von Meyer's (1830) earlier generic descriptions and de Blainville's (1853) specific description of *M. superciliosum*. He created new species for the material collected around Caen in Normandy and three of these (*M. superciliosum*, *M. moreli*, and *M. brachyrhynchus*) include the metriorhynchids found in the English Lower Oxford Clay and contained in the Leeds Collection at the British Museum (Natural History). The characters used to diagnose the species included skull proportions, ornament of cranial bones, relationships of cranial bones, and numbers and types of teeth.

Lydekker (1890) compared an imperfect skull and mandible from Peterborough with Deslongchamps's figures, and concluded that it proved the existence of a separate genus *Suchodus*, with one new species *S. durobrivense*. Fraas (1902) extended the descriptions of *M. brachyrhynchus*, *M. superciliosum*, and *M. moreli* and erected a new species *M. blainvillei* (shown by Wenz (1968) to be synonymous with *M. superciliosum*). Schmidt (1904) created *M. jaekeli* for a specimen from the Oxford Clay which was subsequently also shown by Leeds (1907), Andrews (1913), and Wenz (1968) to be synonymous with *M. superciliosum*.

Andrews (1913) erected three new species for specimens collected from the Peterborough district, which he distinguished from species created by E. E. Deslongchamps, Lydekker, and Fraas. His work was based on the metriorhynchids in the Leeds Collection. He recognized seven species in all (his text-fig. 73) and defined them as follows:

(*a*) Forms in which the surface of the cranial bones is without sculpture:

M. laeve—'A small species with a narrow skull, teeth numerous and close set, upwards of thirty on each side of the mandible.'

M. leedsi—'Skull broader and more massive than in [*M. laeve*]. Teeth large and close set, about thirty-six in each maxilla.'

(*b*) Forms in which the surface of the cranial bones is more or less sculptured with pits and grooves:

(i) Narrow skulled forms:

M. superciliosum—'A narrow skulled form in which the surface of the frontal is sculptured with sharply defined pits. The frontal extends forwards nearly to the level of the anterior angle of the prefrontals, and its length in front of the orbits of the temporal fossae is considerably greater than the least width between the orbits. About twenty eight teeth in each maxilla.'

M. moreli—'A narrow skulled form in which the frontal bears a sculpture of shallow and, as it were, partly obliterated pits, its anterior angle does not extend forwards to the level of the anterior angle of the prefrontals, and its length in front of the temporal fossae is about equal to the least width between the orbits. About twenty-six teeth in each maxilla.'

(ii) Broad skulled forms:

M. cultridens—'Skull with comparatively short rostrum in which the nasals are separated from the premaxillae by a distance about equal to a quarter of their own length. Supraorbital notch an open continuous curve, teeth smooth and with strongly compressed crowns, about twenty teeth in the maxilla.'

M. brachyrhynchus—'Skull with short rostrum in which the nasals meet or nearly meet the premaxillae. The supraorbital notch forms a sharp angle, and a line joining the outer angles of the prefrontals passes behind the posterior angle of the nasals. About twenty-one teeth in each maxilla.'

M. durobrivense—'Skull broad with a short rostrum in which the nasals do not quite reach the premaxillae. A line joining the outer angles of the prefrontals passes through the hinder end of the nasals. About sixteen teeth in each maxilla.'

Wenz (1968), working with Callovian specimens from France, concluded that the metriorhynchids should be arranged in two groups: (i) those species with a narrow, long snout—*M. superciliosum*, *M. leedsi*, and *M. laeve* (in the definition of these species ornament is important); (ii) those species with large skulls and short snouts—*M. cultridens*, *M. durobrivense*, and *M. brachyrhynchus*.

Wenz (1968) noted the degree of individual and age variation amongst the Callovian metriorhynchids, by analogy with variation in living crocodiles (Mook 1921; Kälin 1955). She doubted the value of certain taxonomic criteria employed by previous authors, and later (Wenz 1970) favoured the provisional retention of the species *M. cultridens*, *M. durobrivense*, and *M. brachyrhynchus*.

De Gasparini and Diaz (1977) created *M. casamiquelai* for a *Metriorhynchus* skull from the Callovian of Northern Chile, and included it with the second of Wenz's (1968) groups.

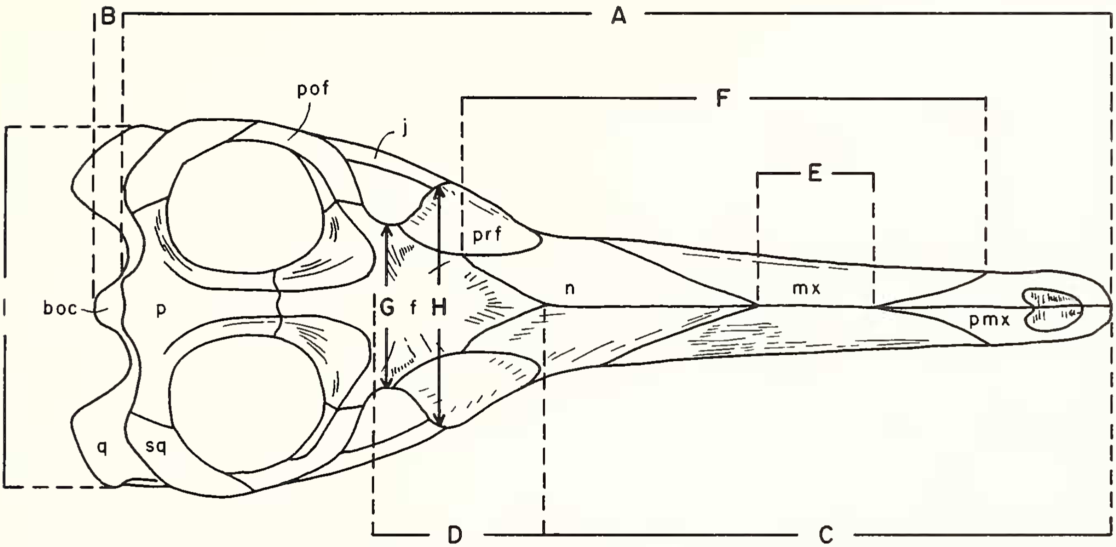
To summarize, the currently accepted species of *Metriorhynchus* from the Callovian are *M. superciliosum* de Blainville, 1853, *M. moreli* E. E. Deslongchamps, 1867, *M. durobrivense* (Lydekker, 1890), *M. brachyrhynchus* E. E. Deslongchamps, 1867, *M. laeve* Andrews, 1913, *M. leedsi* Andrews, 1913, *M. cultridens* Andrews, 1913, and *M. casamiquelai* de Gasparini and Diaz, 1977. The criteria used in the division of the genus by Deslongchamps (1863–1869) and Andrews (1913) were: A, size and proportions of the skull—broad or narrow; B, sculpture of the dorsal surface of the cranial bones—with or without sculpture; C, numbers of teeth; D, relationship between frontal and prefrontal bones; E, distance between the nasals and premaxillae; and F, development of the frontal bone—measured as the projection of the frontal anterior to the supratemporal fenestrae compared to the least width between the orbits. Deslongchamps's and Andrews's specific diagnoses were based on the typological species concept, in that each *Metriorhynchus* species was viewed as being virtually invariable, and small morphological variations were considered to have taxonomic significance. The taxonomy rested upon small samples or individual specimens because morphological standards were established in the type specimen, so that additional specimens were not thought to be relevant to the diagnosis of that species.

Wenz (1968, 1970), de Gasparini and Diaz (1977), and Buffetaut (1977) have all expressed doubts in recent years as to the validity of these taxonomic criteria, but have not suggested any formal revision of the taxonomy because they did not have access to sufficient material on which such a revision could be based.

MATERIAL AND METHODS

The results presented here are based on an extensive study of Callovian *Metriorhynchus* specimens belonging to the Leeds Collection, together with a range of supplementary material. These crocodiles occur principally in the *jason* and *coronatum* zones of the Lower Oxford Clay and were found in a small area of north Cambridgeshire, near Peterborough.

A variety of cranial characters was measured, including those which had been used to diagnose species by



TEXT-FIG. 1. The pattern of dorsal cranial bones in *Metriorhynchus*, showing the measurements taken during morphological analysis (see Table 1). Abbreviations: boc, basioccipital; f, frontal; j, jugal; mx, maxilla; n, nasal; p, parietal; pmx, premaxilla; pof, post frontal; prf, prefrontal; q, quadrate; sq, squamosal; A, length in mid-dorsal line; A + B, length from occipital condyle to tip of snout; C, length from the anterior end of frontal to tip of snout; D, length of frontal anterior to supratemporal fenestrae; E, distance between nasals and premaxillae; F, length of nasals; G, least width between orbits; H, width between outer angles of prefrontals; I, width between outer angles of quadrates.

Deslongchamps, Andrews, and de Gasparini and Diaz, so that information about dissociated metriorhynchid material could be synthesized. In this way the sample size available for analysis was substantially increased (numbers in parentheses) beyond that analysed by Andrews (1913): *M. laeve*, 2 (4); *M. leedsi*, 2 (4); *M. moreli*, 4 (7); *M. superciliosum*, 4 (26); *M. cultridens*, 2 (2); *M. brachyrhynchus*, 2 (4); *M. durobrivense*, 2 (4); and *M. sp.* (34).

The features A–F (listed above) which are currently accepted as having taxonomic validity are evaluated here. A, C, E, and F can be examined quantitatively, B and D qualitatively. Some of these are not, in fact, independent characters. The variation in cranial characters is assessed in the light of the neontological species concept (Newell 1956) bearing in mind the probable levels of individual variation which might occur in a crocodile population (Mook 1921; Cott 1961; Dodson 1975). Where the current criteria are shown to be invalid, appropriate revisions are suggested. The cranial measurements taken are shown in text-fig. 1, and the data so obtained set out in Table 1.

Ranked statistics derived from Table 1, a similarity matrix, and nearest neighbour scores have been tabulated for all specimens allocated a computer number; these tables have been deposited with the British Library as Supplementary Publication No. 14029 (7 pages). It may be purchased from the British Library, Lending Division, Boston Spa, Wetherby, Yorkshire LS23 7BQ, UK. Prepaid coupons for such purposes are held by many technical and university libraries throughout the world.

CHARACTER ANALYSES

Bivariate plots

Combinations of two and three cranial measurements were plotted and their compatibility with the present taxonomic interpretations tested (text-figs. 2 and 3). Text-fig. 3 indicates that two groups of metriorhynchids can be determined, where the groups are based on the relationship between the width of the skull (measured across the prefrontals) (text-fig. 3A) and the separation of the nasals and premaxillae (text-fig. 3B). These results are not entirely compatible with the present classification.

TABLE 1. Cranial measurements in *Metriorhynchus* (see text-fig. 1). Abbreviations: BM(NH), British Museum (Natural History), London; HM, Hunterian Museum, Glasgow; CMP, City Museum, Peterborough; NMW, National Museum of Wales, Cardiff; SM Sedgwick Museum, Cambridge. Computer numbers were allocated to those specimens sufficiently complete for computer analysis. All measurements in millimetres (* denotes estimated value).

	BM(NH) R3015 *M. laeve*	BM(NH) R3014 *M. laeve*	BM(NH) R4762 *M. superciliosum*	BM(NH) R2031 *M. laeve*	BM(NH) R3899 *M. leedsi*	BM(NH) R3540 *M. leedsi*	BM(NH) R2054 *M. moreli*	BM(NH) R2044 *M. moreli*	BM(NH) R2053 *M. superciliosum*	BM(NH) R2030 *M. superciliosum*	BM(NH) R2058 *M. superciliosum*	BM(NH) R2051 *M. superciliosum*	BM(NH) R2041 *M. superciliosum*	BM(NH) R2055 *M. superciliosum*	BM(NH) R2032 *M. moreli*	BM(NH) R3804 *M. cultridens*	BM(NH) R3541 *M. cultridens*	BM(NH) R3700 *M. brachyrhynchus*	BM(NH) R3699 *M. brachyrhynchus*	BM(NH) R3939 *M. brachyrhynchus*
Computer number	**1**	**2**		**3**	**4**	**5**	**6**	**7**	**11**	**12**		**13**	**14**	**15**	**10**	**27**	**28**	**29**	**30**	
A, length in mid-dorsal line	480	450					607	575		634	600	510	522	480*	595	738		615	635	
A+B, length from occipital condyle to tip of snout										660		555	552			772		680	700	
C, length from anterior end of frontal to tip of snout	315			295*	375*	340*	405	372	295							407	304	380*	392	
D, length of frontal anterior to supra-temporal fenestrae	82		75	79	85	93	78	91	70						80	143	105	110	128	145
E, distance between nasals and premaxillae	100	95	80	90	100*	85	74	60	45	90	75	55	55	70	79	58	38	0	16	
F, length of nasals	150	135*		163	194	200	243	225	180	213		200	195	170	206	252	195	250	247	
– length of supratemporal crest	83						124	112								179				
G, least width between the orbits	54	40*	40	57	77	95	84	89	60	81	82	71	67	64	80	123	88	104	105	126
H, width between outer angles of pre-frontals	114	90*	111	109	138	146	148	130	107	150	130	117	114	114		255	166	213	224	233
I, width between outer angles of quadrates				133	180	178	185			185			156	135		254			247	
– mandible length		492					720	635		720			560		670	823				
– length of symphysis							360	270		305					270					

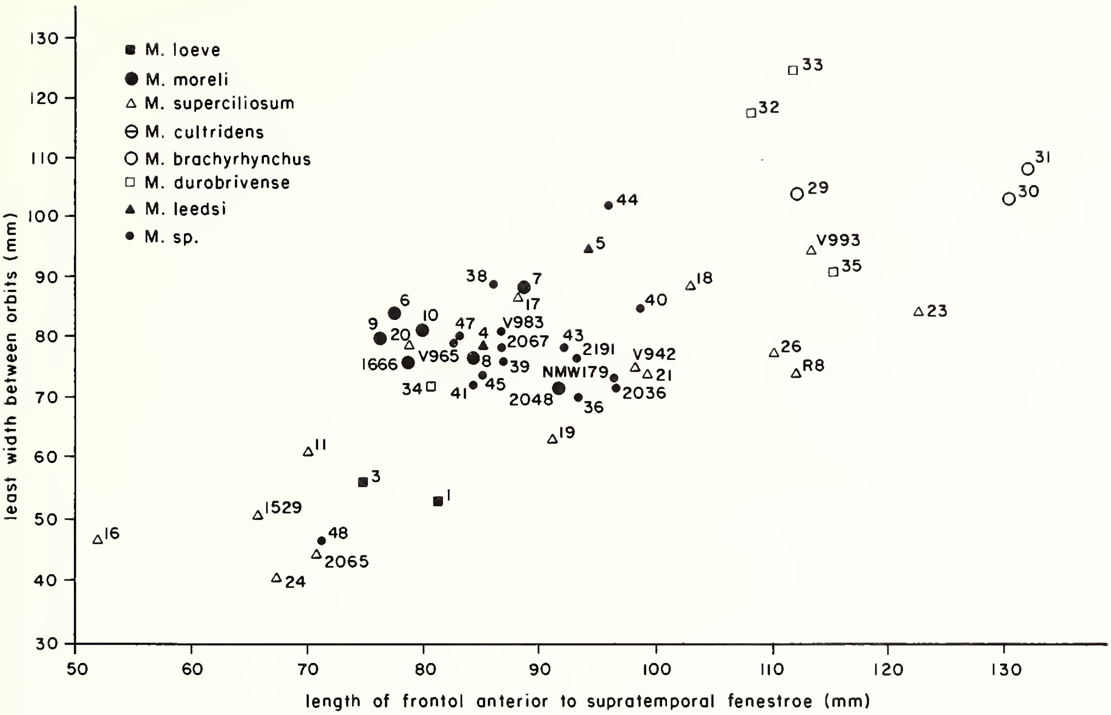
TABLE 1 (*Cont.*)

	BM(NH) R3321 *M. durobrivense*	BM(NH) R2039 *M. durobrivense*	BM(NH) R2618 *M. durobrivense*	CMP R180 *M. superciliosum*	CMP R18 *M. superciliosum*	CMP R20 *M. superciliosum*	NMW C179 *M.* sp.	SM A *M.* sp.	SM B *M.* sp.	SM C *M.* sp.	HM V962 *M.* sp.	HM V963 *M. superciliosum*	HM V964 *M. superciliosum*	HM V965 *M.* sp.	HM V966 *M.* sp.	HM V971 *M. moreli*	HM V973 *M.* sp.	HM V975 *M.* sp.	HM V978 *M.* sp.	HM V981 *M.* sp.
Computer number	**32**	**33**	**34**	**24**	**25**	**26**		**47**	**48**	**49**	**36**	**16**	**17**	**37**	**38**	**8**	**39**		**40**	**41**
A, length in mid-dorsal line			425			530*	600*	596					560	575*	550*	589			494*	
A+B, length from occipital condyle to tip of snout						572*	638*	624					594	615*	583*	639			529*	
C, length from anterior end of frontal to tip of snout			238			322*	370*	406	238	373	366		355	374	350	385			300*	
D, length of frontal anterior to supra-temporal fenestrae	109	112	80	58	91	97	114	82	71	102	91	53	90	84	87	84	87		98	84
E, distance between nasals and premaxillae	18	25	26	58	79	97	84	34	119		106	89		98	62	81			78	
F, length of nasals	196	187	148		233	218	178	174	154	216	216		205*	213	169	253	206*		206	
– length of supratemporal crest				67		111	120	108		117		78	121	115	122	114	117	109	99	118
G, least width between the orbits	119	127	72	41	79	78	77	79	47	83	69	46	87	78	90	77	76*	76	84	73
H, width between outer angles of pre-frontals	229	229	149	81	138	128*	147	139	89	151	140*	85	134	132	136	148	130*	141	150*	129
I, width between outer angles of quadrates				94		189	206	172				104	172		166*	186	188	183	167	170*
– mandible length																				
– length of symphysis																				

Continued

TABLE 1 (*Cont.*)

	HM V982 *M.* sp.	HM V983 *M.* sp.	HM V985 *M. superciliosum*	HM V987 *M.* sp.	HM V989 *M. superciliosum*	HM V998 *M.* sp.	HM V1015 *M. superciliosum*	HM V1140 *M. superciliosum*	HM V1142 *M.* sp.	HM V1143 *M. moreli*	HM V1004 *M.* sp.	HM V1000 *M.* sp.	HM L54498/1	CMP R176 *M. brachyrhynchus*	CMP R19 *M. durobrivense*	CMP R24 *M. leedsi*	CMP R8 *M. superciliosum*	CMP R10 *M. superciliosum*	CMP R17 *M. superciliosum*	CMP R42 *M. superciliosum*
Computer number			**18**	**42**	**19**	**43**	**20**	**21**	**45**	**9**		**44**		**31**	**35**			**22**		**23**
A, length in mid-dorsal line			599	632		563	590*	619	576	595	680*			802						
A+B, length from occipital condyle to tip of snout			631	671		591		657	614		735			853						
C, length from anterior end of frontal to tip of snout			374	412	335*	359	380*	403	384	408				506				418		
D, length of frontal anterior to supra-temporal fenestrae		88	103	91	91	88	79	98	85	76		96		130	114	82		92		99
E, distance between nasals and premaxillae	72		77	50	93	89*	73	84	65	132		89		33				71	84	79
F, length of nasals			232	256	189	206	255	222	214	184		242	260	339*		187		247	229	198
- length of supratemporal crest		98	119	124		108	120*	121	106	103	128	85		166	120		113			127
G, least width between the orbits	79	79	88	92	61	77	78	74	74	80*	92	100	95	111	91		72	79		85
H, width between outer angles of pre-frontals	134	129	145	156	112	133	132	139	129	134*	156	152	174	208	206	122	126	152	164	140
I, width between outer angles of quadrates	172	166	197	204				197	166	177	206*	198	232	283	256	153	165	181		
- mandible length										636										
- length of symphysis										294										



TEXT-FIG. 2. Bivariate plot of least width between orbits and length of frontal anterior to supratemporal fenestrae. Specimens identified by computer number (see Table 1) or, when no computer number exists, by registration number, as follows: V, Hunterian Museum, University of Glasgow; NMW, National Museum of Wales, Cardiff; four digit numbers without prefix, British Museum (Natural History), London. Same species symbols and specimen numbering are used in text-figs. 3–7.

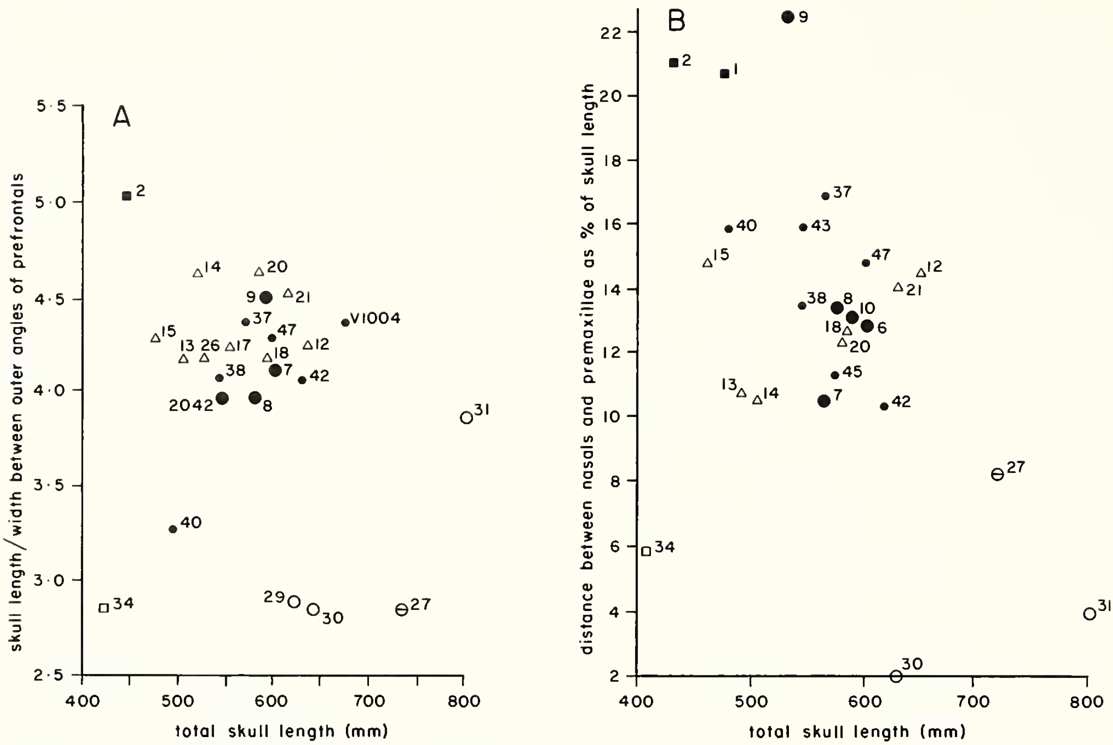
Although a division into two groups seems reasonable on the basis of these characters (the groups correspond to Andrews's 'broad' and 'narrow' skulled species), there is no evidence for further taxonomic subdivision.

The two features compared in character F by Andrews are not independent. The length of the frontal bone anterior to the supratemporal fenestrae and the width of this bone between the orbits together characterize the development of the frontal bone. Furthermore, the degree of this development might be expected to vary between individuals.

A further range of six character combinations for the two groups suggested from text-fig. 3A and B were then examined by ranked ratio and percentage values (Table 2). Two groups are again apparent, defined on the basis of characters 2 and 6, where Group 1 includes *M. leedsi*, *M. superciliosum*, *M. moreli*, and *M. laeve*, and Group 2 includes *M. cultridens*, *M. brachyrhynchus*, and *M. durobrivense*. All other characters measured (see Table 2) show greater 'within group' than 'between group' variation. Thus, characters 2 and 6 may be valid specific characters. Together they quantify an aspect of snout growth, character 2 being a measure of the 'width component' of growth and character 6 an indication of the amount of anteroposterior elongation in relation to broadening that occurred during growth.

Principal coordinate analysis

The quantitative analysis of cranial characters was then extended by the use of principal coordinate analysis, a multivariate technique. In this method, each specimen is defined by a particular array of

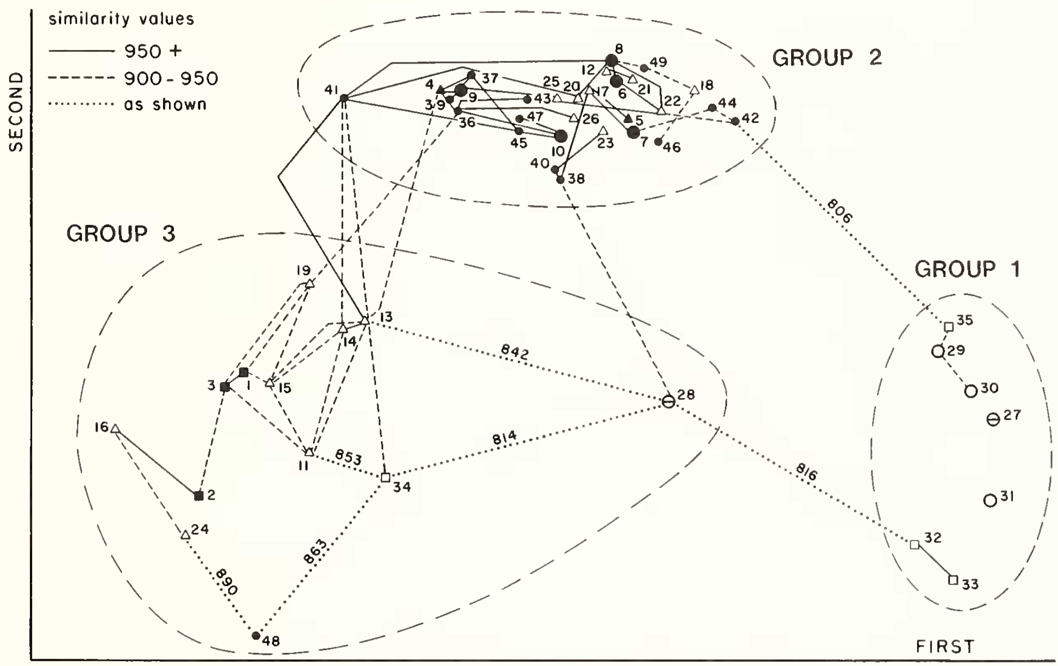


TEXT-FIG. 3. Bivariate plots showing A, skull length/width of skull between outer angles of prefrontals against skull length, and B, distance between nasals and premaxillae as a percentage of skull length against total skull length.

TABLE 2. Ranges in Groups 1 and 2 (see text-fig. 4) of ranked statistics derived from cranial measurements of *Metriorhynchus*.

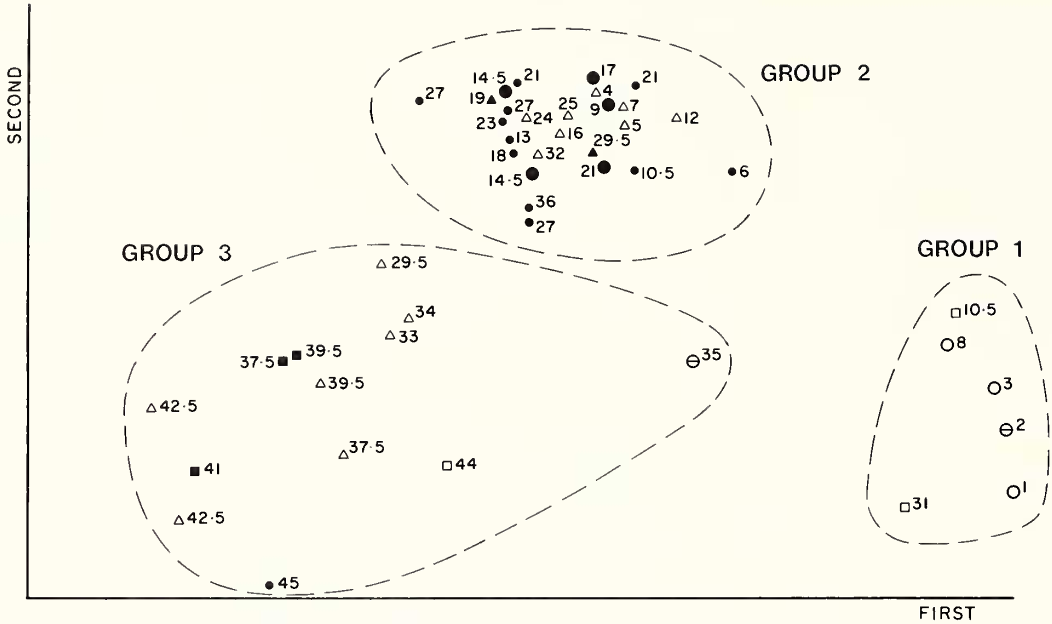
Character	Character number	Range in Group 1	Range in Group 2
Ratio of width of skull (outer angles of quadrates) to length of skull	1	2·80–3·55 : 1	2·83–2·90 : 1
Ratio of width between outer angles of prefrontals to length of skull	2	3·97–5·00 : 1	2·83–3·85 : 1
Distance between premaxillae and nasals as % of total length of skull	3	7·91–22·18 % (= 14·27 %)	0·00–7·85 % (= 7·85 %)
Length of nasals as % of total length of skull	4	Shows continuous range of overlap between Groups 1 and 2	Shows continuous range of overlap between Groups 1 and 2
Length of mandibular symphysis as % of length of mandible	5	Shows continuous range of overlap between Groups 1 and 2	Shows continuous range of overlap between Groups 1 and 2
Distance between nasals and premaxillae as % of length of nasals.	6	19·53–71·73 % (= 52·21 %)	0·00–23·01 % (= 23·01 %)

values (the measured cranial characters). The vectors describing the collection of metriorhynchid specimens can be represented by points in *n*-dimensional space, where *n* equals the number of metriorhynchids in the sample minus 1. The distance between any pair of specimens represents their similarity in terms of all the characters measured. The metric expression of these measures of similarity is the similarity coefficient, and coefficients expressing the relationships between every pair of metriorhynchids were combined together to form a similarity matrix. Projecting the coordinates of the vectors on to the first and second principal coordinates or axes (eigenvectors) highlights the morphological differences that exist between members of the sample, since the first and second axes maximize the variance of the measured characters. The results of the multivariate analysis are shown in text-fig. 4, which illustrates a reasonably convincing clustering into three groups (the relationship of specimens 28 and 34 to Groups 2 and 3 is problematical. These spatial relationships must be a representation of the cranial characters possessed by the specimens.

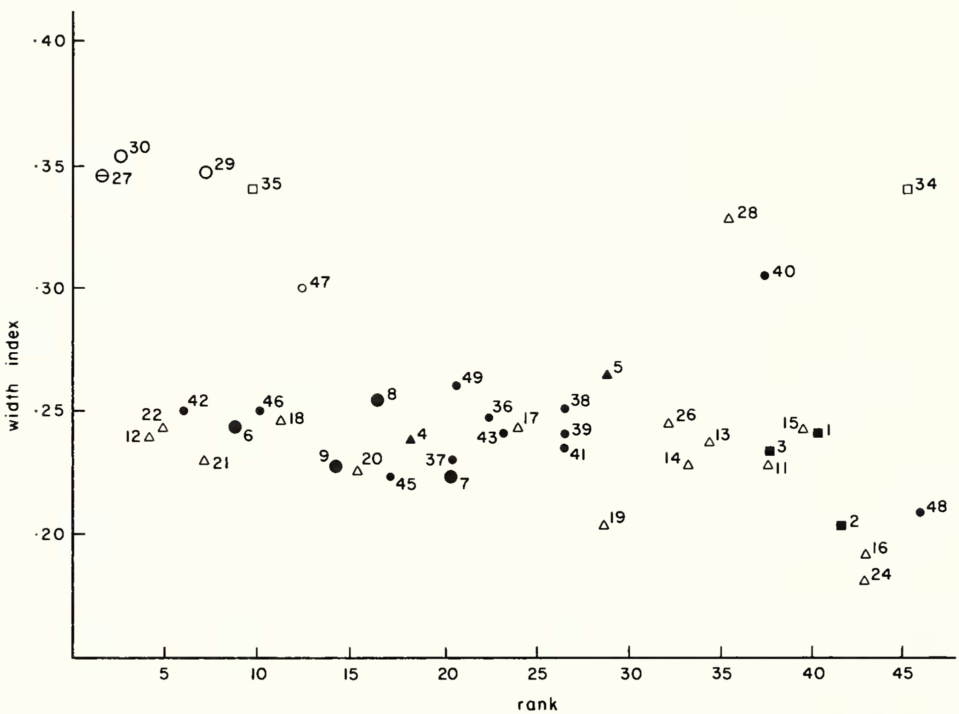


TEXT-FIG. 4. Principal coordinate analysis plot showing spatial relationships on the first and second axes, and similarity values. Specimens denoted by their computer numbers (see Table 1).

Text-fig. 4 shows that a large percentage of Group 2 are linked internally by similarity coefficient values greater than 950 (out of 1000). Marginally lower similarity coefficients link specimens 49, 18, 46, 44, and 42 with each other; these individuals appear to represent a small divergence from the character states possessed by the specimens clustered around the 'norm' for this group. Values between 900 and 950 occur between most of the specimens within Group 3 and, with a similar frequency, between end members of Groups 3 and 2. Group 1 shows an apparently lower level of similarity between its members. This is because there are far fewer individuals to compare with each other in this group, with the resultant smaller likelihood of attaining high levels of similarity (i.e. there is less chance for specimens to approximate to the mean for a given character). The levels of similarity between each specimen and the six 'most similar' specimens to them are shown in the nearest neighbour score charts (deposited with the British Library, see above).



TEXT-FIG. 5. Ranked lengths of specimens shown in text-fig. 4.



TEXT-FIG. 6. An indication of skull 'shape' using a plot of width index against ranked lengths. Specimens denoted by their computer numbers (see Table 1).

The characters which seem to be most significant in separating Groups 1 from Groups 2 and 3 are width of the skull and, to some extent, length of the skull. Text-fig. 5 shows that the most significant factor separating Groups 2 from Group 3 is length of the skull. These apparently decisive characters of width and length of the skull were examined by calculating a 'width index' for each specimen: W/L, where W is the width between the outer angles of the prefrontals, and L is the total length in the mid dorsal line. Where possible, L was estimated for incomplete skulls.

Width index is plotted against the rank values (from text-fig. 5) in text-fig. 6 which confirms that skull width is independent of skull length, i.e. broad and narrow skulls occur at both ends of the ranked series, despite the fact that the majority of broad-skulled specimens available for analysis and which plot in Group 1 (text-fig. 4) are large specimens. The grouping between and within Groups 2 and 3 (text-fig. 4) is therefore a function of size (length), not shape (width). This explains why the similarity values of the links between many of the end members of these two groups are as high as 940–949. Although it is reasonable to assume that size is an indication of individual growth, there is no evidence from skull proportions or suture closure (Mook 1921) to suggest a juvenile status for any of the smaller skulls. Thus, Groups 2 and 3 include metriorhynchids of variable size, but with skulls of similar widths.

Text-fig. 6 identifies specimens 28 and 34 (*M. durobrivense*) as 'broad-skulled' metriorhynchids. Their relationship to the other specimens in Group 1 is complicated by the fact that they are significantly smaller. Since it has already been established that text-fig. 4 measures skull size (length) and skull width, it follows that a marked difference in either character (in this case skull length) will increase the distances between 28 and 34 and Group 1, because distance is, in this sense, a measure of morphological difference.

TAXONOMIC VALIDITY OF CHARACTERS

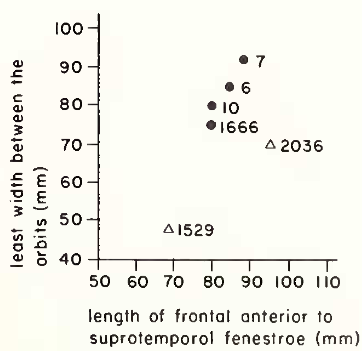
If skull width is truly independent of skull size, and not merely an allometric index in the larger skulls, it is a base on which a classification could be erected. This is in partial agreement with Andrews (1913), who subdivided his narrow-skulled and broad-skulled groups:

Narrow-skulled metriorhynchids

Andrews (1913) used four characters in his subdivision:

1. *Relationship between length of frontal bone anterior to supratemporal fenestrae and its least width between orbits*. Text-fig. 2 shows that the amount of variance of this index between individuals said to belong to the same species is considerable. Andrews justified using this character on the basis of the sample illustrated in text-fig. 7, but it is now clear that these individuals account for only a small percentage of the total variation.

2. *Relationship between frontal and prefrontal bones*. The degree of individual variation shown in text-fig. 8 indicates that this feature should not be considered a valid taxonomic character.



TEXT-FIG. 7. Bivariate plot of least width between orbits and length of frontal anterior to supratemporal fenestrae in specimens of *Metriorhynchus superciliosum* and *M. moreli* analyzed by Andrews (1913).

3. *Ornament of bones of dermal skull roof.* Andrews devised a classification of the 'narrow-skulled' metriorhynchids based on whether the roofing bones were ornamented or smooth. Wenz (1968, p. 31) stated, 'It seems right that among the long muzzle forms we can recognize ornamented forms (*M. superciliosum* and *M. moreli*) and forms without ornament (*M. laeve* and *M. leedsi*) but to push the specific determination further seems hardly satisfactory . . . in fact on most of the specimens examined the variations in ornamentation are minimal . . . moreover there exists a range of intermediaries between the two extremes'. My examination of narrow-skulled metriorhynchids, however, shows that there is continuous variation between 'smooth' and 'faintly ornamented' skulls (see particularly specimens CMP R7 and R72), and those showing dense ornamentation. It is impossible to subdivide this spectrum in any taxonomically useful way.

4. *Number of teeth.* I have found considerable variation in overall numbers of teeth between specimens assigned to the same species by Andrews (1913) and subsequent workers. Variation also occurs between the right and left sides or upper and lower jaw of the same individual. Similar variation was recorded by Wenz (1968).

Kälin (1933) concluded that tooth number varied by only one or two within the various species of living crocodilians which he examined. It is also clear, however, that tooth number was never the sole characteristic used to recognize a species—it always occurred in conjunction with morphological differences in the skull.

There are no differences in tooth form among the Callovian metriorhynchids. All specimens have longitudinally ridged dental enamel with anterior and posterior carinae and pointed crowns. The numbers of teeth are: *M. superciliosum*, 28–30; *M. moreli*, *c.* 26; *M. laeve*, *c.* 30; and *M. leedsi*, 30–36. These variations are in excess of those recorded by Kälin (1933), but it has been shown above that there are no convincing additional differences in either skull form or ornament of the skull bones that can be used to separate these specimens any further.

Broad-skulled metriorhynchids

Andrews (1913) used five characters in his subdivision:

1. *Degree of separation of nasals and premaxillae.* Text-fig. 3B indicates that specimens with the broadest snouts (defined by the distance across the outer angles of the prefrontals) show the least distance between nasals and premaxillae. The separation of these bones is an expression of the degree of antero-posterior growth contrasted with widthways expansion of the rostrum. In the widest skulls, growth has been apparently more concentrated in the expansion of the skull, with consequently less elongation, and since the expression of antero-posterior elongation is the extension of the maxillae, this greater expansion is signified by the reduced distance between the nasals and premaxillae.

Within the broad-skulled metriorhynchids, however, the distance separating the nasals and premaxillae is too variable to be taxonomically useful (see text-fig. 4) and the group does not conform to the relationships expressed by Andrews (1913).

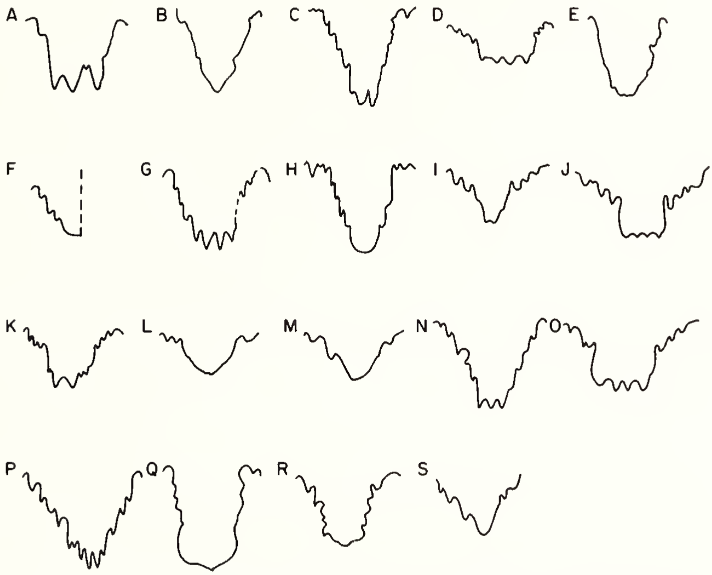
2. *Number of teeth.* The variation is as follows: *M. cultridens*, 20–21; *M. brachyrhynchus*, 18–21; *M. durobrivense*, 16; and *M. casamequalai*, 21. There is no significant or systematic variation in tooth form between these species. The dental enamel is raised into extremely fine longitudinal ridges with smooth pointed crowns. There are, in all cases, fewer but larger teeth in the jaws of the broad-skulled as opposed to the narrow-skulled crocodilians; McIlheny (1976) demonstrated this feature in living crocodilians. It is the result of the reduced development of the maxillae which are the main tooth-bearing elements.

If one argues that all the broad-skulled specimens should be classified as one species, the differences in tooth number are larger than that seen in living crocodilians (Kälin 1933), but there are no other significant morphological differences of the skull which vary together with tooth number (see below) to further subdivide the broad-skulled group. Such a subdivision would be based on tooth number alone.

3. *Length of rostrum.* Assessment of the taxonomic validity of this feature is difficult because the relevant part of the skull is preserved in only a few specimens. The available data suggest that it is

variable within species (Table 1)—as it is in the narrow-skulled metriorhynchids, for which there is a more comprehensive sample size (Table 1). Also, this character is not independent: it is determined by the amount of antero-posterior elongation, as expressed mainly in the length of the maxillae which, in turn, determines the separation of the nasals and premaxillae—and, indeed, the number of teeth (character 2).

4. *Relationship between frontal and prefrontal bones*. Frontal/prefrontal relationships are shown in text-fig. 8, which illustrates their variability and, hence, unsuitability for taxonomic use.



TEXT-FIG. 8. Variation in form of frontal/nasal suture. Distance separating the most anterior point of projection of frontal from prefrontals is indicated. A–G, *Metriorhynchus superciliosum*; A, R2053 (27 mm); B, R1529 (19 mm); C, R2051 (2 mm); D, R6859 (38 mm); E, R1665 (10 mm); F, R2041; G, R2036 (12 mm); H, R1666 (22 mm). I, *M. moreli*, R2044 (31 mm). J–L, *M. laeve*; J, R2031 (11 mm); K, R4762 (18 mm); L, R3015 (22 mm). M, *M. leedsi*, R3899 (6 mm). N, *M. leedsi*, R3540 (19 mm). O, *M. cultridens*, R3541 (28 mm). P, *M. durobrivense*, R2618 (24 mm). Q, *M. durobrivense*, R3321 (18 mm). R, *M. brachyrhynchus*, R3700 (44 mm). S, *M. brachyrhynchus*, R3999 (25 mm). All specimens in BM(NH).

5. *Ornament of dorsal skull bones*. Andrews attached relatively minor importance to this character in his type descriptions of *M. cultridens*, *M. brachyrhynchus*, and *M. durobrivense*; he concluded that its development varied continuously between the three broad-skulled *Metriorhynchus* species he recognized, between individual specimens, and even between different cranial bones for a given specimen.

The ornament on BM(NH) R3804 (*M. cultridens*) is of particular interest; it does not appear to be as strongly developed as Andrews concluded (1913, p. 196) and represents the least degree of development of ornament recorded to date in a European specimen. In this context one of the characters used by de Gasparini and Diaz (1977, p. 357) to define their new species *M. casamiquelai* needs to be re-examined: 'There is no ornamentation (all species in group (b) Wenz (1968) have different degrees of ornamentation)'.

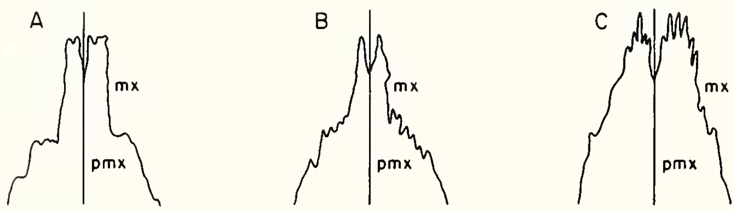
M. casamiquelai

The type specimen of *M. casamiquelai* is in South America, and comparisons here are based upon personal communication with de Gasparini about aspects of morphology.

1. *Ornament*. There is a gradational development of ornament between *M. casamiquelai* and *M. cultridens* (R3804); both show lateral pitting of the maxillae and faint striae on the nasals. Unfortunately a portion of the frontal and prefrontal of *M. casamiquelai* has been restored, thereby reducing the amount of morphological detail which can be retrieved from this vital area of the skull. *M. casamiquelai* appears to support the concept of a continuous range of variation of ornament and provides an example of the very beginnings of the development of that ornament (as do CMP R72 and R7 for the narrow-skulled metriorhynchids).

2. *Cranial sutures*. One other character used by de Gasparini and Diaz (1977, p. 357) merits close examination: 'That the suture separating the premaxillae and maxillae has the shape of an "M", all known species have the shape of a "V" '. The known variability of other cranial sutures suggests that this character is not taxonomically useful. My work has revealed that although some specimens do have an 'M'-shaped suture (text-fig. 9: A, 'broad-skulled'; B, C, 'narrow-skulled'), the 'V'-shaped suture occurs very much more frequently.

All of the characters used by de Gasparini and Diaz (1977) to define *M. casamiquelai* are taxonomically invalid because they exhibit a wide and continuous range of variation.



TEXT-FIG. 9. Form of premaxillary/maxillary suture. A, *M. brachyrhynchus*, R3699. B, *M. moreli*, R6860. C, *M. superciliosum*, R2058. All specimens in BM(NH).

INTERPRETATION OF SKULL WIDTH DIMORPHISM

There are two feasible interpretations of the facts presented above. First, that two species are represented by the specimens studied, corresponding to the 'broad-skulled' and 'narrow-skulled' groups, and that the majority of 'broad-skulled' specimens occupy the top end of the spectrum of skull sizes (lengths). Niche partitioning between these two species would then be a function of their different dietary requirements which, in the fossil specimens, are reflected by a progressive disparity in skull and jaw size and breadth (text-fig. 6; highlighted by specimens 38 and 24 in relation to 35, 29, 30, and 27). The resulting contrast in jaw mechanics would facilitate the taking of a different range of prey (see Cott 1961, table 19 and fig. 34, for different categories of food taken by crocodiles in relation to their size).

The second interpretation is that the 'broad-skulled' and 'narrow-skulled' dimorphism is due to intraspecific variation in skull shape and proportions. Sexual dimorphism in crocodiles has been reported by Cott (1961, p. 252, fig. 16), Neill (1971, pp. 243, 250, fig. 85), and McIlheny (1976, p. 64); their records show that males are, in general noticeably larger than females. This might also be expected to apply to fossil crocodiles, as measured by skull size (Greer 1974). If so, female metriorhynchids would correspond to those specimens which plot on the bottom and mid-left-hand area of text-figs. 4 and 5 (Group 3), while males would correspond to the remainder (Groups 1 and 2); the line between males and females would, of course, be somewhat ill-defined. The explanation of the broad-skulled group in this instance would be that some crocodiles (presumably males?), on reaching a certain skull length, broaden out rather than elongate. Neill (1971, p. 180) documented this feature for living crocodilians, and the evidence in the literature always refers to its occurrence in males (but with no statement that it is exclusive to this sex).

SYSTEMATIC PALAEONTOLOGY

Using the principal criterion of skull width, two species of *Metriorhynchus* have been defined, in which the contrasted growth profiles required to produce the segregation are reflected in characteristic dimensions of and interrelationships between the dermal roofing bones (principally the prefrontals, nasals, premaxillae, and maxillae) and tooth number.

Genus METRIORHYNCHUS von Meyer, 1830, emend. E. E. Deslongchamps, 1867

Type species. Metriorhynchus geoffroyi von Meyer, 1832.

Metriorhynchus superciliosus de Blainville, 1853, emend. E. E. Deslongchamps, 1867

1853 *Metriorhynchus superciliosum* de Blainville, MS Conybeare, figured by Deslongchamps, 1867, pl. 20, fig. 2*a*, *b*, *c*.
1867 *Metriorhynchus moreli* E. E. Deslongchamps, p. 320, pl. 21, figs. 4 and 5; pl. 22, figs. 1 and 2.
1913 *Metriorhynchus leedsi* Andrews, p. 178, text-fig. 73A.
1913 *Metriorhynchus laeve* Andrews, p. 178, text-fig. 73B.

Type data. Location of type specimen from the collection of de Blainville is unclear in Deslongchamps (1867, pp. 306–319, pl. 20, fig. 2*a*, *b*, *c*) and subsequent publications.

Diagnosis. Narrow skull (where ratio of width between outer angles of prefrontals and length of skull falls approximately within 3·97–5·00 : 1) with many close-pointed teeth (*c.* 26–28, but exceptionally more than 30 in each maxilla). Frontal and prefrontal bones show extensive range in development of sculpture and in relationship between their most anterior points of projection. Nasal/frontal suture displays a variety of forms. Development of frontal bone, as illustrated by relationship between its width between orbits and its length in front of supratemporal fenestrae, is individually variable. Nasal and premaxillary bones separated to a variable degree, but never in contact.

Metriorhynchus brachyrhynchus E. E. Deslongchamps, 1867

1867 *Metriorhynchus brachyrhynchus* E. E. Deslongchamps, p. 333, pl. 23, figs. a–d.
1890 *Suchodus durobrivense* Lydekker, p. 285, figs. 2 and 3.
1913 *Metriorhynchus durobrivense* Andrews, p. 179, text-fig. 73G.
1913 *Metriorhynchus cultridens* Andrews, p. 179, text-fig. 73E.
1977 *Metriorhynchus casamiquelai* de Gasparini and Diaz, p. 426, no figure.

Type data. The type material figured by Deslongchamps (1867, p. 333, pl. 23, figs. a–d) was destroyed in the Second World War.

Diagnosis. Broad skull (where ratio of width between outer angles of prefrontals and length of skull falls approximately within 2·83–3·85 : 1) with fewer teeth than *M. superciliosus* (16–20 in each maxilla) but with similar pointed crowns. Varying amounts of sculpture on frontal and prefrontal bones, whose relationship between their most anterior point of projection also varies. Nasals and premaxillae in contact or separated by up to 33 mm (but always less than in *M. superciliosus*).

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